COMPARATIVE ANATOMY OF THE LEAF-BEARING CACTACEAE, II

STRUCTURE AND DISTRIBUTION OF SCLERENCHYMA IN THE PHLOEM OF PERESKIA, PERESKIOPSIS AND QUIABENTIA

I. W. BAILEY [1]

VARIOUS FORMS OF SCLERENCHYMA, as commonly defined (e.g., Eames and MacDaniels,[2] Esau [3]), occur in the leaf-bearing genera *Pereskia*, *Pereskiopsis* and *Quiabentia*: (1) libriform fibers are present in the secondary xylem of stems and roots, (2) strands of aggregated slender fibers in the primary phloem of stems, (3) concentric layers of sclereids in periderm of stems and roots, and (4) highly diversified forms of sclereids in the secondary phloem of *Pereskia*. It is significant in this connection that, under normal circumstances, sclerenchyma does not occur in the leaves and pith of the three genera. The libriform fibers of the xylem and the sclereids of the periderm will be dealt with in subsequent papers of this series. In the following pages, I shall confine myself to a discussion of sclerenchymatous elements that are formed in the phloem of the three genera.

The leaf-bearing Cactaceae have mixtures of very dense and exceedingly soft tissues and are difficult to section. After experimenting with various methods of embedding following preliminary softening with such reagents as hydrofluoric acid, I have in general obtained the most useful preparations by sectioning stems and roots of living plants or specimens preserved in formalin-acetic-alcohol fixative without the use of preliminary treatments. Although the transverse and longitudinal sections thus obtained with an adequately sharpened knife and sliding microtome are relatively thick, they are suitable for critical visual examination. Furthermore, they have the advantage, not only of being obtained simply and rapidly, but also of retaining starch, crystals, and other cell inclusions which may be much modified or eliminated during softening and embedding. It must be admitted, however, that they are not of the best quality for photographic illustration.

FIBERS OF THE PRIMARY PHLOEM

Strands of aggregated primary phloem fibers occur in the stems of *Pereskiopsis* and *Quiabentia*, as well as in those of *Pereskia* (FIGS. 1a,

[1] This investigation was financed by a grant from the National Science Foundation.

[2] Eames, A. J., and L. H. MacDaniels. An introduction to plant anatomy. Ed. 2. McGraw-Hill Book Co., N. Y., 1947.

[3] Esau, K. Plant Anatomy. John Wiley and Sons, N. Y., 1953.

7a). Particularly in the more succulent parts of *Quiabentia* and some species of *Pereskiopsis*, the number of fibers in each strand tends to be reduced. Furthermore, the maturation of fibers in the former genera tends to be precocious, whereas in *Pereskia* the final stages of maturation may at times be delayed until more or less extensive cambial activity has occurred.

The individual fibers are slender, elongated elements of the general external form illustrated in FIG. 12. Their diameter commonly varies from 20 to 50 microns and their length from a few hundred microns to more than 2000. The marked variability in length occurs, not only in strands from different parts of a plant, but also in adjacent fibers of a single strand. Fibers having normal, lignified secondary walls may be internally septate or nonseptate, but they do not store starch as the corresponding septate and nonseptate libriform fibers of the secondary xylem so commonly do. Those of *Quiabentia* and *Pereskiopsis* tend to form relatively thick secondary walls and contain few if any internal septa at maturity (FIG. 13). On the contrary, in the case of *Pereskia*, many of the fibers have thinner secondary walls and are internally septate (FIG. 14). It is significant that part or all of such septate fibers in a strand may ultimately form internally a chain of sclereids having lignified, multilayered walls (FIG. 15). Occasionally, the protoplast of one of the sclereids may divide leading to the formation of two smaller sclereids included within a larger one. This unusual phenomenon of cells-within-cells, which is of infrequent and sporadic occurrence in septate libriform fibers of secondary xylem (FIG. 6) is of considerable interest from physiological and developmental points of view and merits detailed investigation. For example, the two or three successive waves of lignified wall formation indicate that lignification is not necessarily an immediate precursor of loss of potentialities or degeneration of the protoplast as has sometimes been assumed.

The orientation of cellulosic microfibrils in the broad central or S_2 layer of the secondary wall of septate and nonseptate fibers, of both the primary phloem and the secondary xylem, varies from approximate parallelism to the long axis of the cell to helices of varying pitch. Clues to such variations may be obtained by studying the orientation of the slit-like pits, by the distribution of slip-planes, and by examining thin transverse, longitudinal and diagonal sections in polarized light. In FIG. 6, a very thin, perfectly transverse section in polarized light between crossed nicols, the tenuous outer or S_1 layer of the four adjacent fibers is strongly birefringent. The broad central or S_2 is dark, whereas in longitudinal section it is birefringent. This indicates that the orientation of cellulosic microfibrils in the S_2 layer of the secondary wall is approximately longitudinal, as does the orientation of slit-like pits and the distribution of slip-planes visible in longitudinal sections. Internal to the normal S_1 and S_2 layers of the septate fibers in FIG. 6 are transverse sections of the multilayered walls of included sclereids, the cellulosic layers of which are alternatingly birefringent and dark in polarized light. In such transverse sections as

FIG. 6, it is not possible to determine whether the original secondary wall of the fibers has a tenuous S_3 layer or not. It should be emphasized in this connection that these cells-within-cells provide interesting material for analysis by electron microscopy.

Occasionally a cell of prosenchymatous form on the margins of a strand of primary phloem fibers divides precociously before secondary wall formation (FIG. 16). Subsequently such cells may form a chain of sclereids (FIG. 17) comparable developmentally to wood parenchyma strands or the strands of short tracheids that occur in certain of the Pinaceae. (See glossary of terms used in describing woods.[4])

FORMS OF SCLERENCHYMA IN THE SECONDARY PHLOEM OF PERESKIA

Under normal conditions of growth, schlerenchyma does not occur in the cortex and secondary phloem of stems and roots of species of *Pereskiopsis* and *Quiabentia* that I have investigated. In striking contrast to absence in these genera is the occurrence (particularly in larger stems and roots) of more or less numerous and diversified forms of sclereids in the secondary phloem of all species of *Pereskia* (including *Rhodocactus*) of which I have examined adequate material. The form and the distribution of the sclereids is consistently different in three distinct categories of putative species of *Pereskia*.

1. Species with Diffusely Distributed Sclereids in the Secondary Phloem

In *Pereskia aculeata* Mill., *P. pititache* Karw., *P. conzattii* Britt. & Rose, *P. autumnalis* (Eichlam) Rose, *P. nicoyana* Web., *P. weberiana* K. Schum., and *P. diaz-romeroana* Cárd., the sclereids in the secondary phloem of large stems and roots are abundant and diffusely distributed (FIGS. 1–3). In transverse sections, these cells, which vary in diameter from less than 18 to more than 100 microns, have conspicuously multilayered secondary walls which frequently occlude the lumen of the cell. As indicated in FIG. 5, the numerous layers of the secondary wall (which may exceed 50 in the case of the largest cells) are alternatingly birefringent and dark or feebly birefringent in polarized light. (Compare with the internal sclereids shown in FIG. 6.)

As seen in longitudinal sections (FIG. 4), these cells have a much elongated prosenchymatous form, the most slender ones having a length of a few hundred microns, whereas the broadest ones may attain at times a length of more than two thousand microns. In many of these cells the lumen tends to be occluded toward the ends of the cells and to be much reduced in the central part (FIG. 18). However, some of the cells having thinner multilayered walls become septate and may subsequently form a

[4] International Association of Wood Anatomists. Glossary of terms used in describing woods. Tropical Woods **36**: 1933.

chain of shorter sclereids internally. The pits of the secondary wall tend to be restricted to the broadest central part of the cell (FIG. 18) and to be more or less irregularly distributed. It is significant in this connection that many of the pits are of the so-called ramiform type characteristic of many sclereids (FIG. 19). From a developmental point of view, such pits are actually of a coalescing, rather than of a ramifying type, for, the orifices of two or more simple pits in the first-formed layers of the secondary wall unite to form a single opening in the inner or last-formed layers of the wall.

A limited number of sclereids may occur at times in the expanded cortex of much enlarged stems (FIG. 1b). These vary from cubical to various bizarre forms. However, where they have a conspicuously longer axis, it is oriented at various angles and not consistently parallel to the long axis of the stem.

2. Species with Sclereids Aggregated in Longitudinally Oriented Clusters

In large older stems of *Pereskia sacharosa* Griseb., *P. grandifolia* Haw., *P. bleo* DC., *P. corrugata* Cutak, and *P. tampicana* Web. aggregations of sclereids commonly occur in the secondary phloem (FIGS. 7, 8). These aggregations, as seen in longitudinal sections of the stem, are of elongated form, frequently of more or less fusiform outline (FIG. 9), and are oriented parallel to the long axis of the stem. They are composed of sclereids which vary markedly in size, form and complexity of internal structure. Although in general the sclereids have a more or less extensively elongated form (with their major axis oriented parallel to the long axis of the stem), they frequently assume aberrant shapes (FIG. 23), apparently due to pressures exerted by adjacent cells during the earlier stages of their excessive enlargement. In some cases, the sclereids have a thick, lignified, multilayered wall and a much restricted or occluded lumen (FIG. 20). In other cases, the sclereids first form a multilayered wall followed by transverse septation and subsequent differentiation of two, three, or more smaller sclereids internally (FIG. 21). Particularly in the case of the largest sclereids, which may attain a diameter of 200 microns and a length of 1000 microns, the protoplasts of the included sclereids may in turn divide, leading to the formation of a second set of still smaller sclereids (FIG. 22). Such compound sclereids of the cells-within-cell type commonly assume many diverse forms internally depending upon the timing and frequency of internal divisions and upon the frequency of diagonally rather than transversely oriented septa. Therefore, in macerations of the phloem, it may be difficult at times to determine with certainty whether certain of the smaller isolated sclereids developed directly from less expanded parenchymatous elements of the secondary phloem or have been released from large compound sclereids by the disrupting forces of maceration.

Strands of aggregated sclereids, at least in many cases, are infrequent or absent, even in much enlarged roots of this category of pereskias, and commonly do not occur in young stems. Thus, I suspect that such pereskias as *Pereskia bahiensis* Gürke and *P. moorei* Britt. & Rose, which have very large, relatively thin, characteristically pinnately veined leaves, will ultimately prove to belong in this category of species when adequate material of the largest and oldest stems can be obtained and studied.

3. Species with Ordinary "Stone Cells" Aggregated in Massive Irregular Clusters

In both the secondary phloem and cortex of older stems and roots of *Pereskia colombiana* Britt. & Rose, *P. guamacho* Web., *P. cubensis* Britt. & Rose, and *P. portulacifolia* Haw., simple, comparatively small sclereids occur in more or less massive aggregations of irregular form (PLATE IV). As indicated in longitudinal sections (FIG. 11), these aggregations do not have a consistently elongated form oriented parallel to the long axis of the stem or root. Furthermore, the sclerotic masses do not contain large compound sclereids but are composed of ordinary "stone cells" as regards size and form. These typical "stone cells" have profusely pitted, thick, lignified, multilayered walls (FIGS. 24–26). When they have a conspicuous major axis (FIG. 26), it tends to be oriented at right angles to, rather than parallel with, the long axis of the stem or root. It is evident from a developmental point of view that these sclereids differentiate from parenchymatous elements of the cortex and secondary phloem without excessive expansion and without internal septation.

DISCUSSION AND CONCLUSIONS

The occurrence of various forms of sclereids in the secondary phloem of pereskias and the absence of such cells in comparable tissue of *Pereskiopsis* and *Quiabentia* are obviously of some significance from a generic point of view, and parallel the presence or absence of glochids in these leaf-bearing genera. However, such differences must ultimately be considered in relation to close similarities that occur in other cells, tissues, and parts of the plants. Obviously a synthesizing discussion should be deferred to the last paper of this review.

The consistent differences in the form and distribution of sclereids in three distinct categories of pereskias are of considerable taxonomic significance, not only in the discussion of putative genera, e.g., *Rhodocactus*, but also in dealing with putative species and varieties. Evidence from the first category of pereskias is indicative of relationship of *Pereskia aculeata* to *P. diaz-romeroama* and *P. weberiana*, of Bolivia, and likewise to *P. conzattii*, of Southern Mexico, and *P. autumnalis* and *P. nicoyana*, of Central America. Evidence from the second category of pereskias is indicative of affinities between *P. sacharosa*, *P. grandifolia*, *P. bleo*, *P. corrugata*, and *P. tampicana*; that from the third category of pereskias of affinities between *P. colombiana* and *P. guamacho*, of northern South

America, and the West Indian endemics *P. cubensis* and *P. portulacifolia*.

The elongated or prosenchymatous form of the sclerenchymatous elements in the first category of pereskias raises the question whether the cells should be classified as phloem fibers with lignified, multilayered secondary walls or as elongated forms of sclereids. The occurrence of "ramifying" or coalescing simple pits in the thick secondary walls of these cells is a characteristic feature of many sclereids rather than of typical fibers. Furthermore, there are numerous transitions between short and variously elongated sclereids in the second category of pereskias. Admittedly, it is difficult to classify plant cells in rigid compartments, owing to the frequent occurrence of intergrading or transitional forms of morphological characteristics. However, in view of the well-known diversities in the size and form of sclereids (see Foster [5]) I am inclined to refer to more or less elongated cells in *Pereskia* having thick, lignified, multilayered walls with "ramiform" or coalescing pits as elongated forms of sclereids rather than as fibers.

The frequent occurrence of sclereids within fibers of the primary phloem and the formation of successive generations of smaller sclereids within large ones of the secondary phloem provide significant material for physiological and developmental investigations, as well as electron microscopy.

ACKNOWLEDGMENTS

I am indebted to the American Philosophical Society for the loan of a Wild microscope. Since acknowledging the assistance of various individuals in the first paper of this series, I have received material of *Pereskia sacharosa* from Dr. Abraham Willink and of *P. portulacifolia* from Dr. José Jiménez. I am greatly indebted to these individuals for the time and effort involved in securing adequately preserved specimens for me. The drawings in this and the preceding paper of this series were made by Mr. Elmer W. Smith.

EXPLANATION OF PLATES

PLATE I

FIGS. 1–3. DIFFUSE DISTRIBUTION OF SCLEREIDS IN TRANSVERSE SECTIONS OF STEMS. 1, *Pereskia aculeata* [Aw 9912] cluster of primary phloem fibers at A, a sclereid in the cortex at B, × 80. 2, *P. nicoyana* [*Rodriguez 662*], × 80. 3. *P. diaz-romeroana* [*Cárdenas*], × 80.

[5] Foster, A. S. Practical plant anatomy. Ed. 2. D. Van Nostrand Co., N. Y., 1949.

PLATE II

FIGS. 4–6. FREE AND INCLUDED SCLEREIDS. 4, *Pereskia nicoyana* [*Rodriguez 662*], longitudinal section of a stem showing elongated diffusely distributed sclereids in the secondary phloem, × 80. 5, *P. aculeata* [Aw 9912], transverse section of a sclereid in polarized light between crossed nicols, × 260. 6, Transverse section of septate fibers with included sclereids photographed in polarized light between crossed nicols, × 1200.

PLATE III

FIGS. 7–9. AGGREGATED SCLEREIDS OF THE SECOND CATEGORY OF PERESKIAS. 7, *Pereskia grandifolia* [*Castellanos*], transverse section showing two aggregations of sclereids in the secondary phloem, primary phloem fibers at A, × 80. 8, *P. sacharosa* [Tucumán], transverse section of a stem showing aggregation of sclereids in the secondary phloem, × 80. 9, *P. grandifolia* [*Castellanos*], longitudinal section of the secondary phloem showing elongated aggregation of sclereids, × 80.

PLATE IV

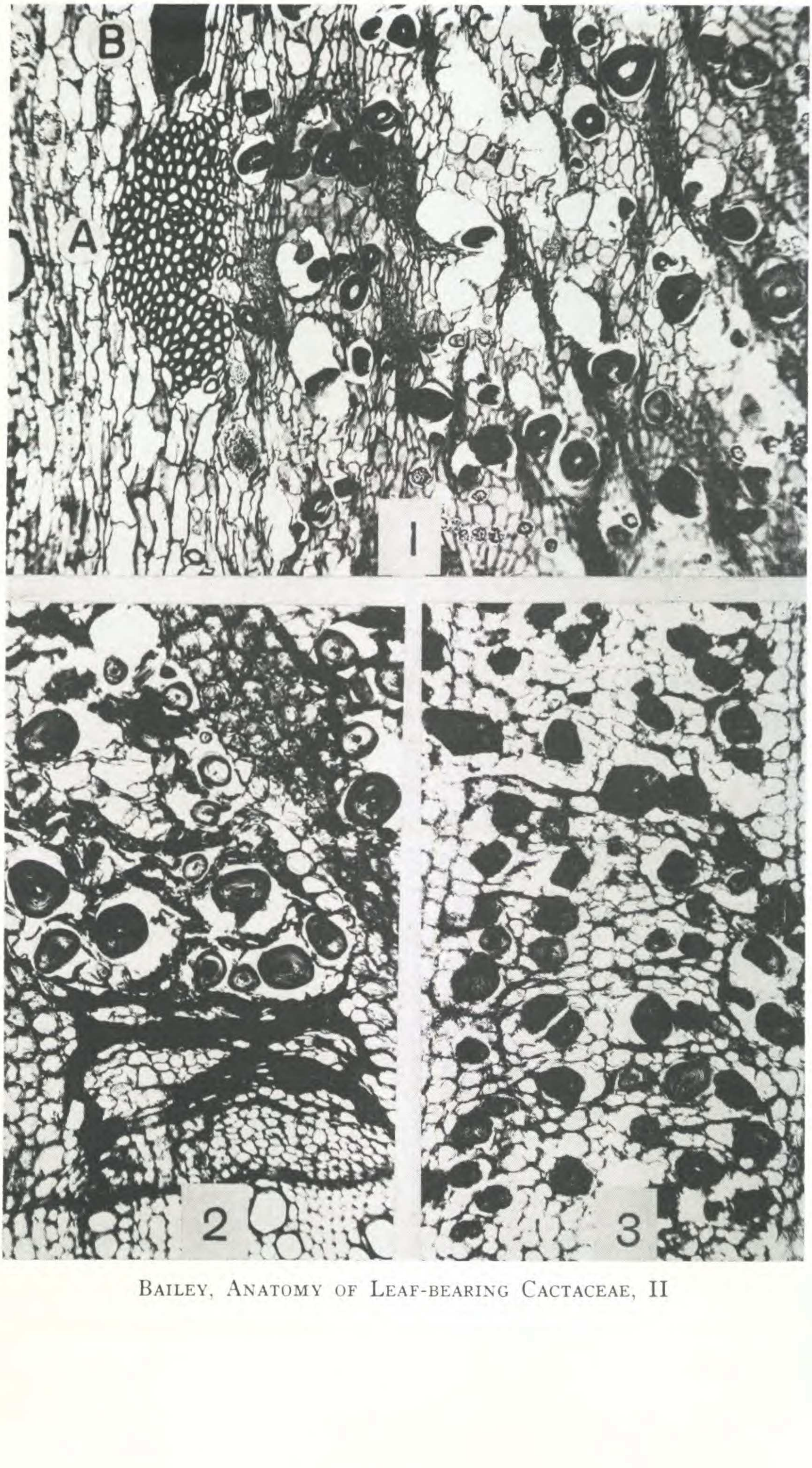
FIGS. 10–11. AGGREGATIONS OF "STONE CELLS" IN THE THIRD CATEGORY OF PERESKIAS. 10, *Pereskia cubensis* [Atkins Garden], transverse section of a root showing massive clusters of sclereids in the secondary phloem, × 80. 11, *P. guamacho* [*Steyermark*], longitudinal section of a stem showing irregular masses of sclereids in the outer secondary phloem and cortex, × 80.

PLATE V

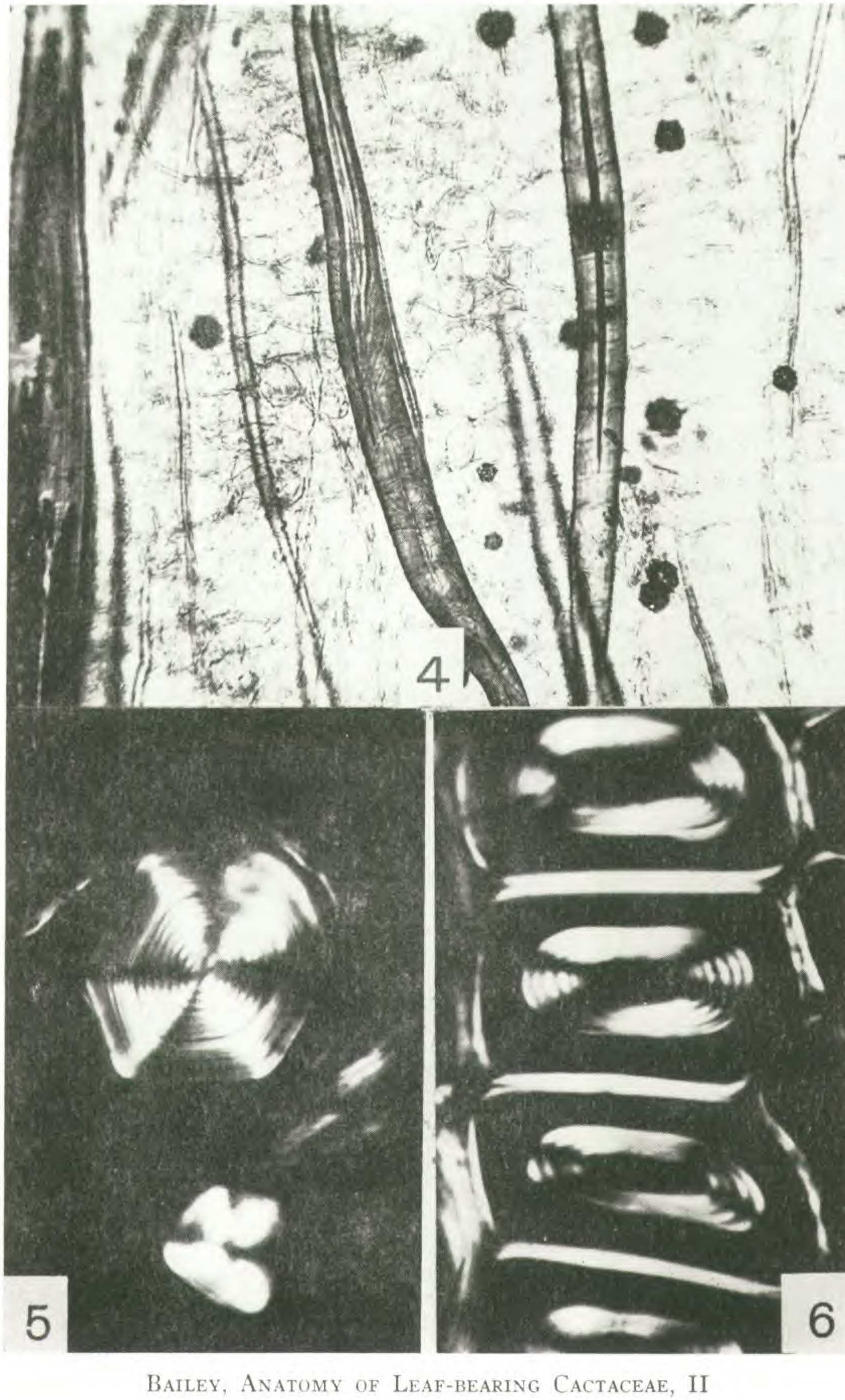
FIGS. 12–17. DIAGRAMMATIC ILLUSTRATIONS OF PRIMARY PHLOEM FIBERS AND SCLEREIDS. Included protoplasts are stippled, primary walls and septa are black, first-formed secondary walls of fibers are white, and the secondary walls of sclereids are multilayered. 12, Characteristic form of immature primary phloem fibers prior to secondary wall formation. 13, Part of a nonseptate fiber having thick secondary wall and reduced lumen. 14, Part of a septate fiber having a relatively thin secondary wall. 15, Part of a septate fiber with included sclereids. 16, Precocious septation of an elongated cell prior to the formation of strand sclereids shown in Fig. 17.

PLATE VI

FIGS. 18–26. DIAGRAMMATIC ILLUSTRATION OF THE FORMS OF SCLEREIDS IN THREE CATEGORIES OF PERESKIAS. Included protoplasts are stippled, primary walls and septa are black, and the secondary walls of sclereids are multilayered. 18, Form of elongated, nonseptate sclereids in the first category of pereskias. 19, Part of the secondary wall of such a sclereid showing "ramiform" or coalescing pits. 20, Single, nonseptate sclereid from an aggregation in the second category of pereskias. 21, Compound sclereid from the same source showing three septa and four included smaller sclereids. 22, Doubly compound sclereid from the same source showing septation of such included sclereids as illustrated in Fig. 21 and the maturation of a second set of still smaller included sclereids. 23, Small laterally deformed sclereid. 24–26, Typical "stone cells" from aggregations in the third category of pereskias.



Bailey, Anatomy of Leaf-bearing Cactaceae, II



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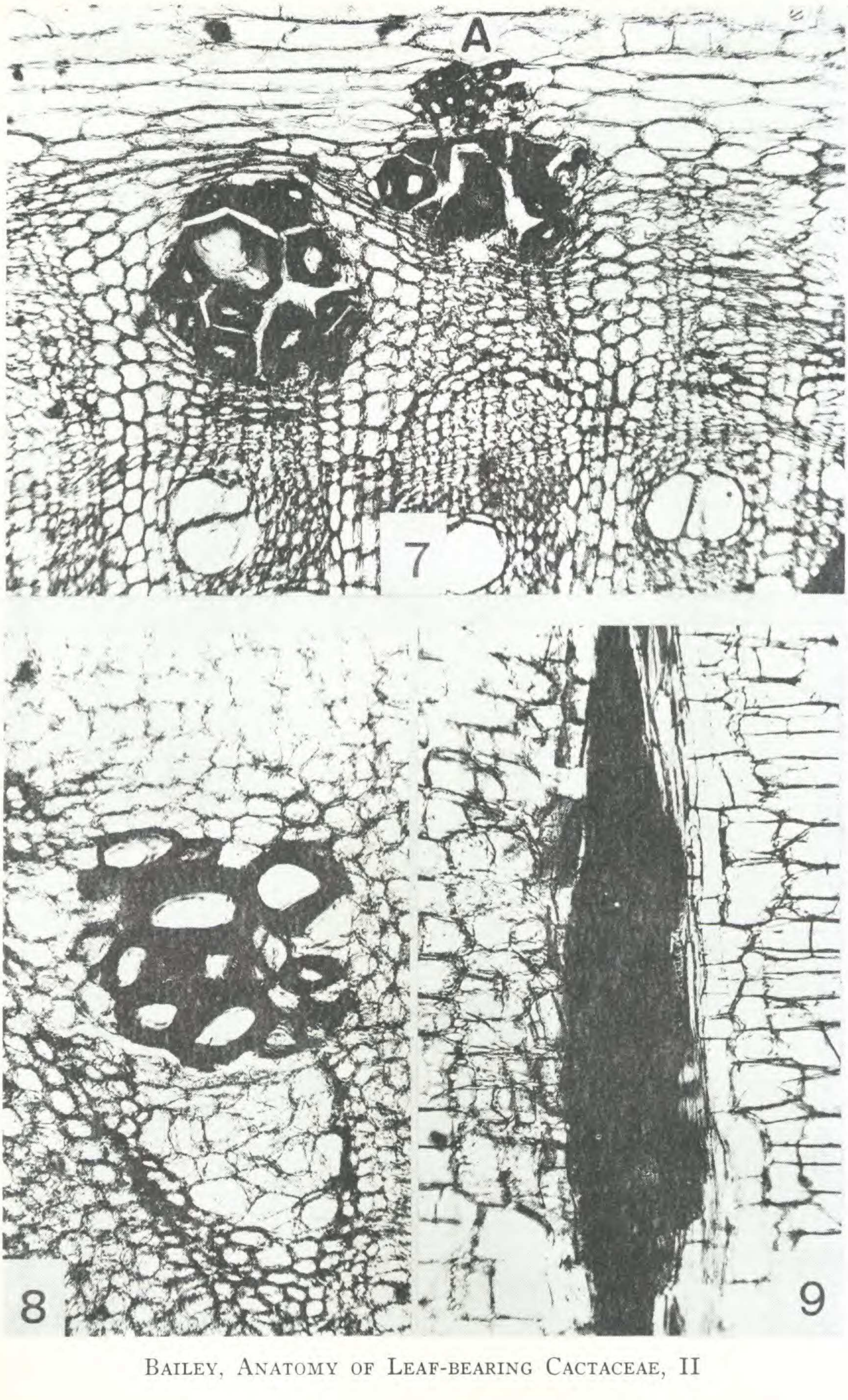

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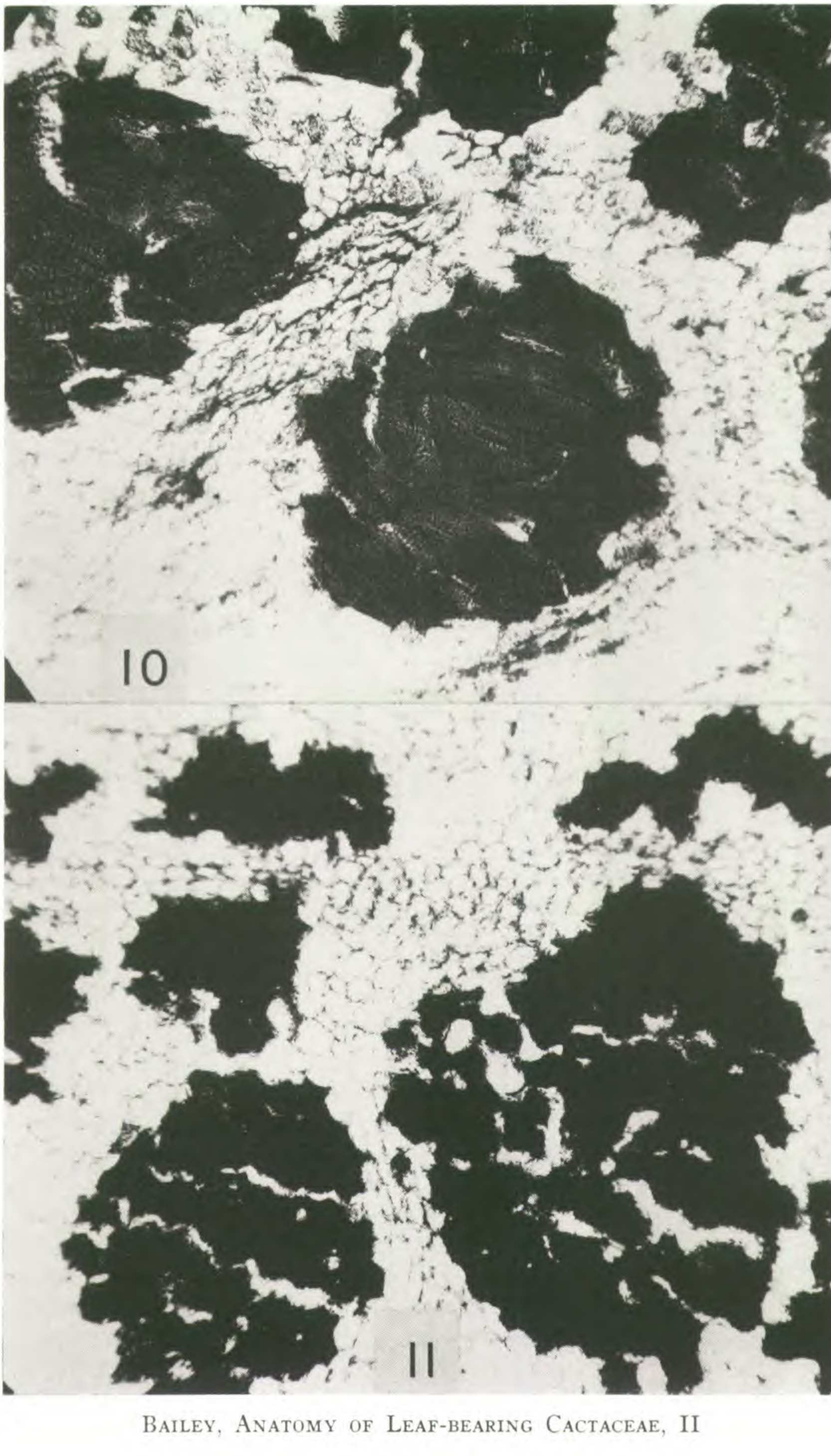

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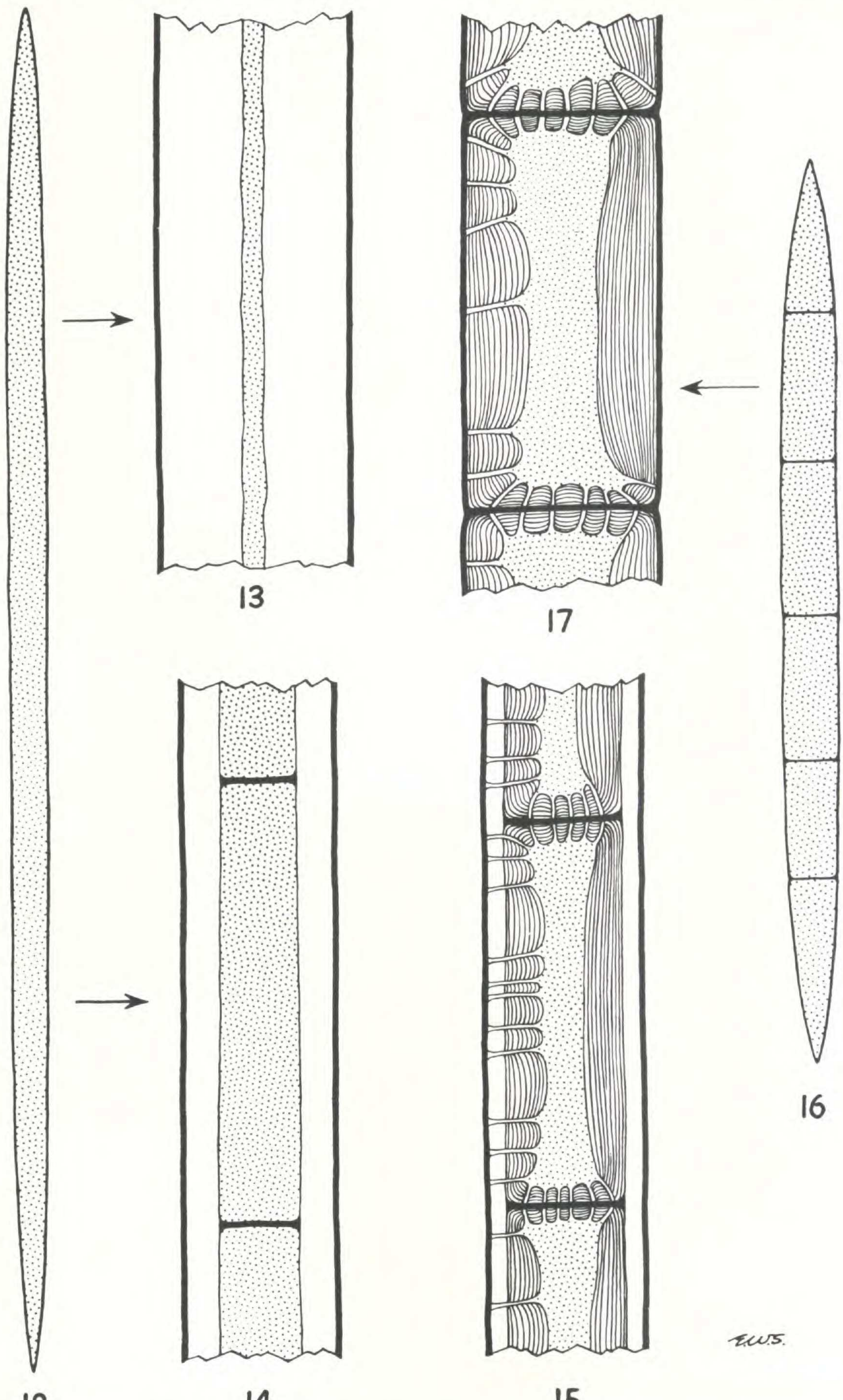

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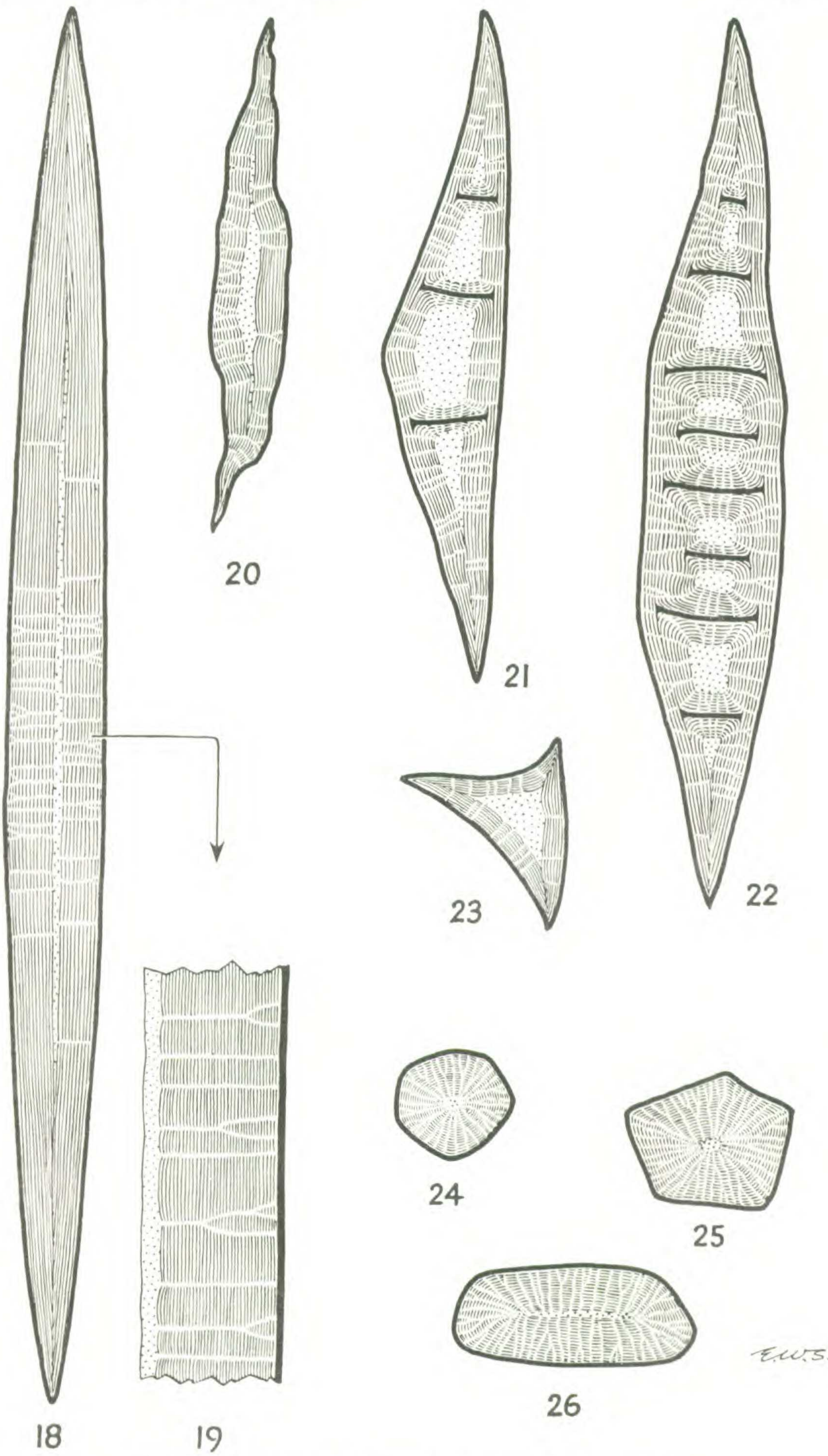

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